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THE EMBRYO SAC OF CASUARINA STRICTA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. L.

THEODORE C. FRYE.

(WITH PLATE XVII)

IN the examination of the embryo sac of Asclepias (2) the writer was impressed with the long resting period of the egg between its fertilization and its first division. The difficulty of distinguishing a fertilized from an unfertilized egg suggested that in some cases in which fertilization was reported to take place after the division of the endosperm nucleus, an error had crept in, an unfertilized egg being mistaken for a fertilized one. If there is fertilization after endosperm division, the fate of the second male nucleus is an equally interesting question. This suggested a reinvestigation of the sac of Casuarina, the results of which are here presented.

The admirable paper of Treub (5) on Casuarina appeared in 1891. In a review of it by Chamberlain (1) in 1896, five years after it was published, the following suggestive statement is made:

> I have been deeply interested in Casuarina's embryo sac without antipodals, as I have been studying Salix and for more than a year was unable to discover any trace of antipodals. However, Salix has antipodals, as some of my preparations now prove. Some slides also show the fushion of polar nuclei to form the endosperm nucleus. There is no doubt that the antipodals of Salix are very transitory, but they are formed nevertheless. It may be that Casuarina has antipodals of this evanescent character. Since the technique betrayed by Treub's figures and text could be greatly improved, I should be glad to see the Casuarina sac studied again in much greater detail, in order that Treub's conclusion may receive additional confirmation or be corrected.

A résumé of the more essential features of Treub's paper is as follows: The species studied were *C. suberosa*, *C. Rumphiana*, and *C. glauca*. The pistillate flowers are naked, occurring in the axils of small bracts that form a cone-like cluster. Each pistil consists of two carpels whose inner surfaces soon fuse along their lower part. Lateral placental outgrowths divide the ovarian cavity into two loculi, but from this central placenta two ovules usually arise, both of which, except in rare cases, form in the same loculus. The funiculi are curved downward so that the ovules lie with the chalaza in the base of the loculus and the micropyle toward the style. Several hypodermal cells ("primary mother-cells"), possibly archesporial in nature, become deeply situated on account of their own transverse divisions and form a multicellular sporogenous tissue, sharply differentiated laterally, as in pteridophytes. Later it is also well differentiated toward the micropyle, but not in the region of the chalaza, where a strong "intercalary growth" takes place, suggesting the origin of sporogenous tissue from cells not arising from the primary sporogenous cells. Of the sporogenous cells,[1] some function as spore mother-cells, some remain small and are soon resorbed, while in some species others become tracheids, recalling the formation of elaters among the liverworts. Those that function as spore mother-cells divide, each forming a row of four. Thus with pteridophytic sporogenous tissue, there is spermatophytic arrangement of megaspores. Some of these enlarge, forming embryo sacs, as many as a score of sacs being counted in a single ovule. They elongate more or less antipodally, some even penetrating the chalaza to the funiculus. Differing from almost all other spermatophytes, the functionless megaspores of Casuarina are not resorbed, but remain among the fully developed embryo sacs. Whatever the number of ovules in an ovary, only one is fertilized. The sacs in the unfertilized ovules enlarge, become binucleate, but form no antipodal prolongations. In the fertilized ovules not all the megaspores that enlarge form prolongations; those not centrally placed are often arrested early. In the fertile ovule only one sac is fertilized.

The formation of cells within the sac was not definitely traced,[2] but developing sacs with one nucleus, and sometimes with two nuclei, were found. A certain nucleus, of unstated origin, near the micropylar end, is itself the egg, or develops the sex apparatus of one to four cells, usually three, one of which is the egg. The others (synergids), it is thought, are homologous with the neck cells of gymnosperms and pteridophytes. Treub draws this conclusion from their origin from a single micropylar cell with cellulose wall, and from their appearance. There are no antipodals.

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[1] Treub applies the term "sporogenous" cells to the tissue both before and after the formation of megaspores.

[2] It will be remembered that this work was done twelve years ago.

This was the first case of chalazogamy reported. The passage through the chalaza is facilitated by the presence of the prolongations of the sterile megaspores, into which the tube enters, leaving them to reach the egg apparatus that is to be fertilized. It is stated, however, that the tube never enters the fertilized sac, but becomes attached to it at some point between the egg apparatus and the antipodal region. Sometimes a nucleus was observed in the tube, but never more than one.

The egg remained unchanged for some time before its fertilization. The exact moment of fertilization was not determined, but before it occurred the formation of a large number of endosperm nuclei had taken place, even as many as fifty. This conclusion was based on the fact that sacs were found which formed endosperm before the pollen tubes reached them.

Casuarina thus shows a megasporic sporogenous tissue reminding one of the pteridophytes, a number of embryo sacs suggesting gymnosperms, and "synergids" suggesting the canal cells of gymnosperms; and it was unique in the route of the pollen tube. These considerations led Treub to believe that the Casuarinaceae are intermediate between angiosperms and gymnosperms.

The species that I studied was *Casuarina stricta* Ait. The material was collected in California from introduced trees by Mr. Albert C. Herre and identified by him. It was killed in chrom-acetic acid; but unfortunately the pieces were large, and hence the killing was not rapid enough to catch cells in mitosis. Only the pistillate cones were secured. The ovaries were carefully teased out with needles and sectioned in paraffin. Longitudinal sections 5 μ thick and stained with safranin and gentian-violet were found to be the most satisfactory. The work was almost all done at night. Light was obtained from a gas lamp provided with a Welsbach mantle, and passed through an eight-inch globe filled with a half-saturated aqueous solution of copper sulfate. In this connection I wish to acknowledge my obligation to Mr. Alexander G. Ruthven and Miss Myrtilla M. Cook for assistance in the preparation of slides, etc.

The young cones, about 5^{mm} long, are covered with what appear to be hairs, but upon examination these prove to be the ends of the filiform carpels. The ovaries are flattened laterally, in contrast to the adaxial flattening of the wings in Pinus. The carpels show numerous crystals in a stratum of cells near their inner surfaces, a condition quite similar to that figured by Treub in *Casuarina suberosa.* The origin of the placenta was not traced, but the ovules arise laterally from a central placenta near its base, as Treub has reported in other species.

The two integuments arise normally (*figs. 1, 2, 18*) and leave a micropylar opening to the nucellus. About the time of their origin one would expect to find the archesporium. In the hypodermal layer at this stage there are certain cells (*fig. 3, a*) which may be interpreted as archesporial, but such an interpretation rests alone upon the form and size, and the relation of cells in that vicinity to each other later; the usual stains would not differentiate the cells either by darker stain or by showing larger nuclei. From *fig. 4* it seems that the archesporial cells divide by walls parallel to the surface. Possibly this is the division into primary wall and primary sporogenous cells, but there is only the evidence of other plants, which is insufficient. Mitosis in the succeeding divisions of cells *b*, *fig. 4*, showing presence or absence of reduction in chromosomes, would settle it, but no spindles were found. However, by further division of cells *a* or *b* or both, in *fig. 4*, a stage like *fig. 5* is reached. More transverse walls and greater elongation result in rows of cells being formed (*fig. 6*), of which the outer ones form the wall tissue and the inner ones the sporogenous tissue. The general arrangement of cells in rows, and the relative position of sporogenous tissue with regard to sterile tissue in comparison with the same in other spermatophytes, especially in the anthers, and in Selaginella, lead me to surmise that cells *a* and *b* of *fig. 4* give rise, respectively, to wall tissue and sporogenous tissue. The occurrence of massive sporogenous tissue, as reported by Treub, is an indubitable fact. Its limits are well defined laterally by the larger cells and larger nuclei of the sporogenous tissue. At the ends it grades more or less into the surrounding parenchyma, and the cells near the microple appear younger than those toward the chalaza. I am inclined to believe that the nucellus as it elongates carries with it the primary sporogenous cells, each of which leaves behind by its own division a train of sporogenous cells. The formation of sporogenous tissue near the chalaza from other than sporogenous cells, as suggested by Treub, was not observed, and is believed not to occur in *C. stricta*. According to Treub, some of the sporogenous cells absorb others, but nothing of the kind was found in *C. stricta.* Either this species differs from those studied by him, or the absorption of sporogenous cells has been confounded with the absorption of megaspores. *C. stricta* forms no tracheids in the sporogenous tissue, agreeing in this with Treub's report for *C. suberosa*. The cells of the sporogenous tissue are several times as long as wide (*fig. 6*), while later, when the embryo sacs begin to form, only approximately isodiametric cells are apparent. This makes me believe that Treub was right in his statement that the formation of four megaspores occurs here. A further reason for my conclusion, and a stronger one, is that later groups of four in a row are recognizable (*figs. 8, 9, 10*).

The differentiation of megaspores begins quite soon after their formation. Usually one of each group of four starts, but sometimes more (*figs. 10, 14*). Many get no further than an enlarged nucleus, while others reach various stages of development, up to an apparently fertilizable sac. A row of four, as in *fig. 10*, certainly presents a strong argument, if any further argument is required, for the megasporic nature of the cells composing such a row in angiosperms. The sterile megaspores are not all resorbed; but some certainly are, and it seems to me that most of them are. The number of sacs reaching maturity varies greatly in different ovules, but ranges from two to twelve. These are mostly those of central location, forming an axial core in the megasporic tissue.

The embryo sac passes through the normal 1, 2, 4, and 8-celled stages (*figs. 9, 10, 14, 15*). These stages were not all seen in sacs which eventually become fertilized, for among so many sacs which reach maturity one cannot tell which will be the favored one until it is approached by the pollen tube. However, if one finds all these stages in embryo sacs arrested in various degrees of development, one may with reason conclude that the one later fertilized passed through the same stages, especially since some which remain sterile reach a development equal to that of the one later fertilized, so far as could be determined. As many as twelve, each having a fully developed egg apparatus, were found in a single ovule.

Within well-developed sacs three cells are organized at the micropylar end, forming the egg apparatus (*figs. 14, 16, 17*). In *fig. 14, C*, the cells have not yet collected definitely enough to make it certain which will form the egg apparatus. It is surmised, however, that three of the cells *a—d* will function as such; *e* is probably the antipodal polar. From *figs. 10, 14, 15, 16*, I can see no escape from the conclusion that the egg apparatus is normal in its origin. These figures are not exceptions chosen here and there to prove a point. They can easily be duplicated. *Fig. 16* is indeed the type of a fully developed sac in this species. An examination of the egg apparatus in *figs. 15, 16, 17* shows that there is considerable variation in the form of the cells composing it in the different sacs. The egg itself cannot be distinguished from the synergids in most cases. Sometimes cases occur showing less than three cells in the egg apparatus, but these are few in number, and it seems to me do not warrant a conclusion that Casuarina is different in this respect from other angiosperms.

Normally there are three antipodals. Comparing *figs. 10* and *14*, the latter is evidently the older group of megaspores. What is seen in *fig. 14, C*, is just what would be expected in the development of a normal sac. Of the eight cells in *fig. 14, C*, three (*f*) are collected in a depression in the antipodal region, just as one might expect, and about them is massed a quantity of protoplasm almost, if not completely, separated from the rest of the protoplasm of the sac, strongly suggesting the separation of these cells by a wall. Comparing now *fig. 14*, *C*, with *fig. 15*, a slightly older sac, the antipodals in the latter certainly cannot be questioned. The whole sac is typical enough of angiosperms to serve as a conventional prefertilization sac. However, as has been remarked, *fig. 16* is more typical of the sac of *C. stricta*. In the older sacs (*figs. 16*, *17*, *20*) these antipodals resemble the unabsorbed megaspores very much, and could easily be mistaken for them. This might account for their reported absence, unless other species differ in this respect from *C. stricta*.

Sometimes, however, no antipodals were found (*fig. 21*), and the reason for this may be considered. Some of the sacs develop long antipodal prolongations (*figs. 14*, *17*, *20*), and these do not always appear at the same time. *Fig. 11*, *a* shows one already under way when the sac is in the 2-celled stage, and 4-celled stages were also found showing the beginning of antipodal prolongations. *Fig. 13* may be developing one at *a*, although that cannot be said with certainty. In a case like *fig. 11*, when the sac reaches the 8-celled stage and the antipodals settle at some point, where will they likely be found? If they seek the antipodal end, they will likely slip into the antipodal prolongation and perhaps be found somewhere within that. At least such a thing seems quite possible. The antipodal prolongations, however, are long tortuous tubes, very much entangled with their fellows. It is almost impossible to trace a definite one to its end with certainty. Much more is it difficult to determine the number of nuclei within, when above and below it are scattered unresorbed undeveloped megaspores. There are nuclei within these prolongations in some cases in which antipodals are wanting, but I was not certain of the number in any case. However, in one case there were three cells (*fig. 14*, *D*, *h*, *i*, *j*) at various distances down the tube. If in this sac the polars had already united, all the nuclei are accounted for. Sometimes, however, the antipodal prolongations are not formed until late in the history of the sac (*figs. 14 C*, *15*). If it occurs after the antipodals have become inclosed by walls and perhaps adhere to the walls of the sac (*fig. 16*, *a*), their presence in the body of the sac, notwithstanding the presence of an antipodal prolongation, is explained. Thus I believe we have the solution of the antipodal problem in Casuarina. Some of the antipodal prolongations grow so long that they penetrate the chalaza, occasionally passing slightly beyond it into the funiculus.

The location of the polar nuclei is quite various. Like the antipodals, they seem occasionally to pass into the antipodal prolongations (*figs. 14 D, 17*), and are lost in the maze of tubes. Sometimes only one was found (*fig. 16, e*), but in this case the polars may have fused and this is the endosperm nucleus. The sac then, except for the antipodal prolongation and its consequent effect upon the location of the antipodals and the endosperm nucleus, seems to be normal in its development.

Only one pollen tube penetrates a flower, hence only one ovule is entered and only one embryo sac in that ovule is fertilized. The favored sac was in all the observed cases near the micropylar end of the megaspore group. The pollen tube enters the ovule as Treub has stated (5). Coming down the central placenta (*fig. 18*), it wanders somewhat in the region where the funiculus has its origin, as though the attractive influence, or whatever it is that guides it, were not sufficiently strong to guide it with certainty. The tubes again frequently branch just before entering the chalaza (*fig. 18, b*). Sometimes the branches reach the surface, as Treub says, and he suggests two possible reasons for the branching: (*a*) for aeration; this is suggested by their often reaching the surface; (*b*) for holdfasts to anchor the tube firmly before it makes its entry into the nucellus. Neither of these appeals to me very strongly, and for the latter I see no reason at all. The cause is probably the same as that which causes wandering at the point of entry into the funiculus.

The tube seems to enter the prolongation of one of the embryo sacs and thus finds an easy passage through the chalaza. The plugs of cellulose in the tubes at intervals, as reported by Treub, are quite rare in *C. stricta*, and when present are short, resembling more a thick transverse wall than a plug. In the maze of tubular antipodal prolongations I was not able to follow the pollen tubes with certainty, and cannot therefore say whether the end is separated from the main body, as Treub claims, or not. When it approaches the sac that it ultimately fertilizes, it is sometimes free (*fig. 20*), and sometimes apparently within the prolongation of the very sac whose egg apparatus it is destined to reach (*fig. 21*). I doubt whether there is any fixed path within the nucellus for the tube. It probably follows the path of least resistance so long as it leads in the direction whence comes the guiding stimulus, whatever that may be.

The sperms were observed near the chalaza in several preparations, as small rounded nuclei accompanied by the tube nucleus (*figs. 18, 19*). They were again seen, still spherical, in the tube near the sac about to be fertilized (*fig. 21*), and here too the tube nucleus was close behind them. This nucleus is easily distinguished from the sperms by its comparatively large size. In *fig. 20* the sac, which is evidently quite near the point of fertilization, shows only two antipodals, and there is one nucleus missing in the egg apparatus. The nuclei *p* are probably the two polars. It would be possible to regard these as two endosperm nuclei, but no reason for doing so appears.

Fig. 21 is a case of "double fertilization." In this the tube, or its contents, apparently entered by way of the antipodal prolongation. The sperms are crescentic bodies, one slightly larger than the other. The two polar nuclei have not yet united. I see no reason for any other interpretation of the two polars; if they are endosperm nuclei, we have a unique case in the fusion of a sperm with endosperm. Which of the three micropylar nuclei is the egg I cannot say, but it is probably the one containing the larger spherical nucleus, or that containing the elongated nucleus. No antipodals are in evidence, but they are probably in the antipodal prolongation. The sperms evidently elongate within the sac or very near it, as in Asclepias (**2**).

I am convinced that no such endosperm formation before fertilization occurs as Treub thought, and my reasons are as follows:

1. The cases of fertilization observed (*figs. 20, 21*) show no endosperm.

2. The pollen tube sometimes enters the ovule before the embryo sacs are ready for fertilization. In one case pollen

tubes were found in the funiculus before the division that results in the four megaspores, and at various times tubes had passed the chalaza while there was no sign of endosperm in the sacs. Usually when a tube gets close to the sac its penetration is rapid, and Treub says its growth within the nucellus is rapid. It seems, then, that there would not be time for a great development of endosperm between the time of the entry of the tube into the chalaza and its entry into the sac.

3. Inferring the exact time of fertilization from the presence of pollen tubes is not conclusive. Anyone who has tried to distinguish a pollen tube in the confused strand of tubular antipodal prolongations will readily understand the difficulty of determining without a doubt what is tube and what is sac. Even if tubes are seen, it is not an easy matter to tell whether they are young or old, and it must have been much more difficult with teased preparations.

4. Very little was said or known twelve years ago about the retarded division of the egg. Now it is known that the angiosperm egg often rests for a time after its fertilization, while the formation of endosperm begins at once. It was the writer's good fortune to study such a phenomenon in the embryo sac of Asclepias (**2**), in which the exact time of fertilization was observed, and the egg rested after fertilization until the endosperm had passed its 16-celled stage. If the exact time of fertilization had not been seen, one would have been apt to judge the resting fertilized egg to be an unfertilized one, and would have been inclined to say that endosperm division took place before fertilization. Johnson's study of the Piperaceae (**3**) has brought to light the same resting period in the egg of *Piper medium*. He figures a sac with twenty-two endosperm nuclei in cross-section, already walled off, and the egg still undivided. In the same paper he says of *Heckeria umbellata* that the embryo sac becomes filled with cellular endosperm before the egg divides. It is only fair to add, however, that fertilization was not observed in these species, but the appearance of the egg leaves little doubt of its fertilization long before it divides.

5. The fact that Treub found a definite wall about the egg in

most cases suggests a post-fertilization stage. The rounded form of his figures of eggs also suggests the same.

Unfortunately, the material at hand showed no embryos nor endosperm, the oldest showing that the pollen tubes had reached the sac. It would have been quite interesting to note the condition of the egg during endosperm development. But if one supposes that Treub mistook a fertilized egg for an unfertilized one—a thing which might even be possible with the technique of today, to say nothing of twelve years ago—and if he further mistook a discharged pollen tube for an undischarged one, the formation of endosperm before fertilization would be eliminated from his own account. It will be recalled here that he himself could not be certain about seeing nuclei in the pollen tube except in a few cases, and in no case is more than one suggested. From the size of the tube nucleus (*fig. 20, t*) one is led to conclude that he saw it rather than a sperm.

A summary of my results with *C. stricta*, as compared with Treub's with *C. Rumphiana*, *C. glauca*, and *C. suberosa*, may be stated as follows:

There is agreement as to the bilocular ovary, the presence of two ovules in an ovary and both in the same loculus, the presence of two integuments and a micropyle, the upright ovules that arise laterally from the central placenta, the multicellular archesporium consisting of a hypodermal plate of cells, the massive sporogenous tissue, the division of each spore mother-cell to form four megaspores, the numerous mature sacs in an ovule, the long antipodal prolongations of the sacs, the fertilization of only one embryo sac in every ovary, and chalazogamy.

There is disagreement as to the origin of the sporogenous tissue, in *C. stricta* all of it arising from the hypodermal archesporial plate, while Treub believes that some sporogenous tissue near the chalaza does not arise from this plate; as to the resorption of sporogenous cells, which Treub claims, but I was not able to observe; as to the sequence in the formation of the embryo-sac structures, which differs in no way in *C. stricta* from the sequence usual among angiosperms; as to the character of the egg-apparatus, which differs in no way in *C. stricta* from that of other angiosperms; as to the presence of antipodals, which are certainly present and normal in number in *C. stricta;* as to the relation of endosperm formation to the time of fertilization, Treub reporting much endosperm before fertilization, and in *C. stricta* fertilization clearly taking place before endosperm-formation.

The additional facts, not observed by Treub, are the occurrence of "double fertilization," and the presence of two sperms, spherical in the pollen tube and crescentic in the sac.

My thanks are due to Professor John M. Coulter and Dr. Charles J. Chamberlain for valuable assistance in the prosecution of the work and in the publication of the results.

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EXPLANATION OF PLATE XVII.

All drawings were made with a Bausch & Lomb camera lucida, $\frac{2}{3}$, $\frac{1}{6}$, $\frac{1}{12}$ (oil) objectives, and nos. 1 and 2 oculars. The figures have been reduced one half, but the original magnifications are given.

Casuarina stricta Ait.

FIG. 1. Young ovule: *n,* nucellus; *i,* inner integument; *l,* loculus without ovule. × 207.

FIG. 2. Ovule: *n,* nucellus; *o,* outer integument; *i,* inner integument. × 140.

FIG. 3. Nucellus about same stage as in *fig. 2; a,* cells which may be archesporium. × 1366.

FIG. 4. Nucellus with hypodermal periclinal wall-formation, suggesting that *a* may be primary wall cells, and *b* primary sporogenous cells. × 1366.

FIG. 5. Nucellus, suggesting that interior cells *r* arise from hypodermal cells at apex. × 1366.

FIG. 6. Nucellus: *s*, massive sporogenous tissue within, with well defined lateral limits. × 900.

FIG. 7. Spore mother-cell about to divide, showing chromatin threads; the cells are longer, the section is diagonal. × 1950.

FIG. 8. Row of four megaspores; *m*, micropylar end. × 1950.

FIG. 9. Row of four megaspores, the middle ones enlarging; *m*, micropylar end. × 1950.

FIG. 10. Row of four megaspores in various stages of embryo sac formation; *m*, micropylar end. × 1950.

FIG. 11. Two-celled embryo sac; antipodal prolongation (*a*) already begun. × 1950.

FIG. 12. Two-celled embryo sac; *m*, micropylar end; no well defined antipodal prolongation. × 1950.

FIG. 13. Four-celled embryo sac; *a*, possibly beginning of antipodal projection. × 1950.

FIG. 14. Row of four megaspores derived from one spore mother-cell and older than those in *fig. 10; m*, micropylar end; *A*, arrested megaspore; *B*, megaspore probably arrested after some internal cell division, but now disintegrating; *C*, 8-celled sac; *a*, *b*, *c*, *d*, will probably form egg apparatus and micropylar polar; *e*, probably antipodal polar; *f*, antipodals with suggestion of wall formation; *D*, 7 or 8-celled sac with antipodal prolongation: *h*, *i*, *j*, probably antipodal and polar or endosperm cells. × 1950.

FIG. 15. Eight-celled embryo sac; *a*, antipodal; *p*, point where antipodal projection may be expected to arise; *po*, polar nuclei. × 1950.

FIG. 16. Typical embryo sac without the long antipodal prolongation; *e*, endosperm nucleus; *a*, antipodals. × 1950.

FIG. 17. Embryo sac with more elongated cells in egg apparatus; only two antipodals found; *a*, polar nuclei or one endosperm and the other antipodal. × 1950.

FIG. 18. Pollen tube approaching the nucellus; *b*, branch of tube; dotted line bounds sporogenous tissue. × 140.

FIG. 19. Part of *fig. 18* enlarged; *t*, tube nucleus, *s*, sperms. × 1366.

FIG. 20. Pollen tube just having reached the embryo sac; *pt*, pollen tube; *t*, tube nucleus; *s*, sperms; *a*, antipodals; *p*, polars, one nucleus in egg apparatus and one antipodal missing. × 1950.

FIG. 21. A case of double fertilization; *s*, sperms; antipodals not found in this preparation. × 1950.